Germination of Seeds of Antelope Bitterbrush, Desert Bitterbrush, and Cliff Rose

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ABSTRACT

Antelope bitterbrush, desert bitterbrush, and cliff rose are among the most important browse species on western rangelands; however, artificial establishment of these species generally has not been successful.

One major reason for this lack of success is the amount and type of dormancy found in the seeds of all three species. The germination of seeds of antelope bitterbrush has probably been subject to more investigations than any other wildlands plant. The nature of dormancy and the natural germination ecology of the species are relatively well known. Dormancy of seeds of these shrubs is broken under natural conditions by cool-moist stratification.

In the case of antelope bitterbrush, the enhancement of germination is closely associated with the caching activities of rodents. To enhance germination before artificially seeding these shrubs, land managers can stratify seeds or treat them with thiourea or hydrogen peroxide.

For each of these species, the authors compared the germination obtained with these three treatments with that of untreated seeds. Germination temperature profiles were constructed using 55 constant and alternating temperatures. The germination profiles for the three species were then compared to seedbed temperatures found on sagebrush (*Artemisia*) rangelands during spring germination.

Even with optimum enhancement, the germination of these seeds will rarely exceed 60 percent. The overall optimum temperature regime for all three species was 10°C for 16 hours and 20°C for 8 hours in each 24-hour period. Researchable alternatives for the germination ecology of these species are discussed.

KEYWORDS: Range revegetation, wildlife habitat, temperature profiles, germination enhancement.

CONTENTS

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GERMINATION OF SEEDS OF ANTELOPE BITTERBRUSH, DESERT BITTERBRUSH, AND CLIFF ROSE

By James A. Young and Raymond A. Evans[1]

INTRODUCTION

Antelope bitterbrush [*Purshia tridentata* (Pursh) DC.], desert bitterbrush (*P. glandulosa* Curran.), and cliff rose [*Cowania mexicana* var. *stansburiana* (Torr.) Jeps] are valuable browse species on western rangelands and are closely related members of the Rosaceae family. Antelope bitterbrush occurs on about 1.4 million ha in the 11 Western States and southern British Columbia (Hormay *1943*).[2] Desert bitterbrush and cliff rose occur on the southern edge of the distribution of antelope bitterbrush from California east to New Mexico, extending into Mexico. Natural hybridization occurs among the three species where their ranges overlap (Blauer et al. *1975*). Antelope bitterbrush is one of the most important browse species for both domestic livestock and wildlife (Nord *1965*). In many areas, communities of this browse plant have deteriorated, and land managers have attempted to revegetate rangelands by planting bitterbrush seed. Although cliff rose and desert bitterbrush have a more restricted distribution compared with that of antelope bitterbrush, they are an economically important species where they occur.

One major hindrance to seeding all three species is dormancy of the seed. Many land managers and scientists have recognized the problem and, as a result, the seed and seedbed ecology of antelope bitterbrush has been subject to research for 45 years. A bibliography of antelope bitterbrush literature, done over a decade ago, lists over 200 citations, many of which mention or are solely concerned with germination and seedbed ecology problems (Basile *1967*). A more recent annotated bibliography (Clark and Britton *1979*) also stresses the importance of seed and seedbed ecology for bitterbrush. The germination and establishment problems probably are as important to the regeneration of desert bitterbrush and cliff rose as they have been demonstrated for antelope bitterbrush, but much less research has been devoted to these species.

The result of all this research effort has been the development of a partial understanding of the nature of the dormancy of antelope bitterbrush seeds and a rather detailed understanding of the natural germination ecology of the species.

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[2]The year in italic, when it follows the author's name, refers to Literature Cited, p. 37.

Nature of Dormancy

When the embryos of antelope bitterbrush "seeds" are dissected from the achenes, the embryos will germinate, indicating the dormancy is controlled by factors associated with the seedcoat and/or pericarp. Embryo dissection has been used as a quick viability check for antelope bitterbrush seeds (Nord *1956*).

Conflicting terminology has been used to describe the fruits of bitterbrush; for clarification, we will define the terms we use before proceeding with a review of the nature of dormancy. The perfect yellow flowers of antelope bitterbrush are borne singly at the end of short lateral leafy spurs. The fruit is an oblong achene about 6 to 12 mm long. The achene consists of the embryo or miniature plant, radicle, hypocotyl, and cotyledons covered by the seedcoat and pericarp. The pericarp, or ripened wall of the ovary, is soft and bright red when the seed is forming, but becomes very dark at maturity. The achene is dry and flinty when mature, and we will refer to it as a seed. When the seed of antelope bitterbrush is mature, it falls from the plant with a papery covering composed of remnant flower parts and tipped with a remnant of the style. Desert bitterbrush seeds have the same covering except the beaked style remnant tends to be more elongated. The seeds of cliff rose are completely enclosed in a thickened, funnelform remnant of flower parts and are tipped by long, feathery styles. Before entering commerce, the papery covering of bitterbrush seeds is normally rubbed free of the seed. The thickened covering of cliff rose seeds cannot be mechanically removed without damaging the seed. When we refer to a cliff rose "seed," the entire assemblage is included. Generally, when sold in commerce, the seeds of cliff rose have the feather style removed.

The seeds of antelope bitterbrush are largely dormant at harvest. Usually, 5 to 20 percent of a seed lot will germinate without germination enhancement. Germination of antelope bitterbrush seeds is greatly enhanced by cool-moist stratification. This treatment simply consists of placing the seeds in a moist environment at a temperature too cold to allow germination. The term "stratification" originated from the forestry practice of placing seeds between layers of peat moss to form a stratified bed for winter chilling. The usual rationale given for germination enhancement from stratification is that the cool-moist period allows sufficient oxygen to reach the embryo to allow germination. We will expand on this concept in a later section on stratification.

Dormant antelope bitterbrush seeds do imbibe water. The seedcoat and pericarp do not interfere with moisture imbibition as is the case with hard-seeded legumes.

In addition to stratification, thiourea treatment can remove the inhibition to germination of antelope bitterbrush seeds (Pearson *1957*). Thiourea belongs to a class of compounds called sulphydryls, a number of which have a markedly stimulatory effect on dormant seeds (Roberts *1973*). In solution, thiourea is in equilibrium with the iso form: $NH_2\ CSNH_2 \rightleftarrows NH_2\ C(SH):NH$. One peculiarity of these compounds is that they can have an extremely narrow concentration range for optimum activity. Thiourea enhancement of antelope bitterbrush germination is an ideal solution to dormancy as far as land managers are concerned. After soaking the seeds in the thiourea solution, they are dried. When the dried seeds are rewet after planting in the field, the thiourea is effective in en-

hancing germination. In contrast, once antelope bitterbrush seeds, or those of most other species, are stratified, the seeds must be planted immediately for the germination enhancement to be effective. If the stratified seeds are dried, not only is the advantage gained by stratification lost, but the seeds become inviable. As we will discuss in detail in a later section, three problems are associated with the use of thiourea treated bitterbrush seeds: (1) the treatment has never been as effective in producing established stands in the field as laboratory results would indicate, (2) thiourea is a highly toxic substance to humans that also produces cancer in laboratory animals, and (3) thiourea-treated seeds must be seeded in the spring. Very little information is published about the response of cliff rose and desert bitterbrush seeds to thiourea, but in one trial, cliff rose seed germination was enhanced by thiourea treatment (Alexander et al. *1979*).

Antelope bitterbrush seeds respond with increased germination when treated with solutions of hydrogen peroxide (Everett and Meeuwig *1975*). Hydrogen peroxide is another compound that has been shown to enhance the germination of seeds of numerous species (Crocker and Barton *1953*). Another major group of compounds that have been shown to enhance germination are the gibberellic acids. Gibberellin has been used to substitute for the stratification requirements of antelope bitterbrush seeds (McConnell *1960*).

Many land managers who have worked with seeding of antelope bitterbrush in the field believe seeds stored at cool to cold temperatures for a year germinate better than freshly harvested seeds. This response would be similar to an afterripening requirement although such requirements usually do not respond to storage temperatures.

In summary, the seedcoat and/or pericarp of antelope bitterbrush seeds interfere with the germination of these seeds. This interference can be overcome by cool-moist stratification or by treatment with various chemicals, all of which have been shown to influence the pentose phosphate pathway of dormancy (Roberts *1973*).

Natural Germination Ecology

When mature, the seeds of antelope bitterbrush fall from the parent shrub encased in the remnant papery flower part. This papery covering largely inhibits germination if the seeds are germinated in petri dishes (Hormay *1943*). If the seeds were allowed to remain in the natural seedbed, presumably strict dormancy would be imposed until this papery covering rotted away, which probably occurs over winter. This is not the case in natural situations because almost the entire crop of antelope bitterbrush seeds is collected by Heteromyid rodents and *Pogonomyrmex* harvester ants (Young and Evans *1978*). When the rodents collect the antelope bitterbrush seeds, they remove the papery covering before caching several tens of seeds in tight clusters buried about 5 cm deep in the surface soil. Accumulation of duff and litter discourages rodent caching activities (Sherman and Chilcote *1972*). These caches remain in the soil over winter, and the seeds receive natural stratification. In the early spring, the cotyledons of the germinating seeds form tight, rose-purple rosettes, identifying the cache locations. The rodents return to graze on the cotyledons. The

cotyledons are rich in carotene and often are vital in the diet of the rodents (for examples of similar situations, see Beatley *1967* and Latourette et al. *1971*). If the rodents fail to return and graze the seedlings, they will die from intraspecific competition. Sloppy grazing by the rodents allows an occasional seedling to escape and establish as a new plant. This is a highly complex regeneration system, which can be easily influenced by human activities but is hard to direct. Rodent populations rapidly respond to changes in plant cover and composition associated with grazing. Seed caching depends on the quality of the seedbed. Before antelope bitterbrush seeds can be cached, they have to be produced, and seed production is highly dependent on the physiologic status of the plants and environmental conditions during flowering and seed set (Nord *1965*).

Considering the natural stratification of antelope bitterbrush seed, it would seem logical to seed untreated seeds in the fall and let nature take its course. Fall seedings of antelope bitterbrush have often proved unsuccessful because of rodent predation on the seeds; however, stands have been successfully established by this method. Heteromyid rodents collect the planted seeds for caching and other types of rodents collect the seeds for direct consumption. Considerable research has been done and currently is under way to develop repellants to protect antelope bitterbrush seeds from rodent predation. Until these treatments are perfected, land managers are forced to spring seeding of antelope bitterbrush seeds that have their germination enhanced by stratification, thiourea, or hydrogen peroxide treatments.

PURPOSE

Our purpose in this study is to compare, at a wide range of constant and alternating temperatures, the germination of untreated, stratified, and hydrogen peroxide- and thiourea-treated seeds of antelope bitterbrush, desert bitterbrush, and cliff rose.

MATERIALS AND METHODS

We compared four basic germination treatments for antelope bitterbrush, desert bitterbrush, and cliff rose seeds. The treatments were: (1) control with no treatment before the seeds were incubated, (2) thiourea soaking before incubation, (3) hydrogen peroxide soaking before incubation, and (4) cool-moist stratification before incubation. The details of each treatment are given in subsections.

In all treatments, four replications of 100 seeds were used. Unless otherwise specified, we collected seed in northern Nevada for antelope bitterbrush or purchased seeds from southwestern Utah for desert bitterbrush and cliff rose during the summer that they were produced and began testing in October of the same year. Seeds were stored before testing in paper bags in the laboratory. Usually, the seeds were hand threshed to avoid injury. The papery flower parts that persist around the achenes of antelope and desert bitterbrush were removed. The indurate portion of the funnelform flower of cliff rose that persists around

the achene was not removed. Seeds were placed on a single thickness of germination paper in petri dishes and kept moist with tapwater. Seeds were considered germinated when the radicle emerged 0.5 cm. The seeds were incubated in dark germinators.

Control Profiles

To develop profiles of the germination of seeds of each species in relation to temperature, we incubated the seeds at 55 constant and alternating temperature regimes. Constant regimes consisted of 0°, 2°, 5°, and then, at 5° increments through 40°C. Alternating regimes consisted of 16 hours at each constant temperature alternating with 8 hours at each higher temperature in the profile daily. For example, 0°C alternated with 2°, 5°, 10°, 15°, 20°, 25°, 30°, 35°, and 40°C while 35°C alternated with 40°C only.

The effects of constant and alternating temperatures on each species in terms of germination percentage was statistically analyzed using a quadratic response surface. This quadratic response surface was composed of a series of regression equations, one for each cold period (16 hours) temperature through the series of warm period temperatures (8 hours) with calculated values and their confidence limits (Ott *1977*).

Thiourea

WARNING! Before considering any seed treatment with thiourea, remember it is a highly toxic chemical that has been linked with the occurrence of cancer in laboratory animals. The regulations of most public land management agencies prohibit the use of this material as a dormancy breaker.

Seeds of antelope bitterbrush, desert bitterbrush, and cliff rose were soaked in 0-, 0.5-, 1-, 3-, and 5-percent solutions of thiourea for 1, 5, 10, 15, 30, 60, and 120 min. Following soaking, the seeds were drained and allowed to dry before incubation.

Based on the results of the preliminary study, we soaked the seeds of all three species in a 3-percent solution of thiourea for 30 min, allowed the seeds to dry, and then incubated them at the standard 55 constant and alternating temperatures used for germination profiles.

Stratification

Stratification--Temperature and Duration

We placed plump, undamaged antelope bitterbrush, desert bitterbrush, and cliff rose seeds between germination blotters in petri dishes. Blotters were used instead of sand, so that the seeds could be readily examined during stratification. The blotters were moistened with water and placed in the dishes in dark germinators. Temperature regimes were -4°, -2°, 0°, 2°, 5°, and 10°C for 1 through 12 weeks.

After stratification, seeds that had germinated were counted. The plates were transferred to a 15°C dark germinator, from which seedlings were removed weekly through 4 weeks. Seeds with white, apparently healthy radicles that emerged 5 mm in length were considered germinated.

Osmotic Stress During Stratification

Aqueous solutions of 0, -4, -6, -8, and -12 bars of osmotic potential were prepared by dissolving appropriate amounts of polyethylene glycol (mol wt. 1,620) in water. Antelope bitterbrush seeds were placed in plastic boxes with ground polystyrene and the various osmotic solutions, following the procedures of Young et al. (*1968*). The boxes were kept at 2° or 5°C in incubators for 10 and 14 days. At the end of the stratification period, we removed the seeds from the boxes, rinsed them briefly under tapwater, and placed the seeds on germination pads in petri dishes. The dishes were incubated at 15°C, and germinating seedlings were counted weekly through 4 weeks.

Soil Matric Potential During Stratification

We used a 15-bar, ceramic plate, soil moisture extractor to obtain soil-matric potentials of -4, -6, -8, and -12 bars in fine sand and clay soils. After the soils reached the desired equilibrium in the extractors, they were transferred to plastic boxes. Antelope bitterbrush seeds were planted 0.5 cm deep in the firmly packed soil, and the boxes were sealed. The boxes were weighed at the beginning and end of stratification to determine if moisture was lost. The boxed soil and seeds were stratified at 2° and 5°C for 10 and 14 days. At the end of stratification, the soils were carefully moistened to near saturation, and the opened boxes were incubated at 15°C. Emerging seedlings were counted weekly through 4 weeks, then the remaining seeds were dug up and checked for germination.

Temperature Profiles

Standard 55 temperature regime profiles were conducted for antelope bitterbrush, desert bitterbrush, and cliff rose using seeds that had been stratified for 2 weeks at 5°C.

Hydrogen Peroxide

Antelope Bitterbrush

Seeds used in these experiments were collected near Boise and Twin Falls, Idaho; northern Ada County, Idaho; and near Reno and Jiggs, Nev., in 1974.

Initial Experiment

Using all five seed sources, we repeated the techniques reported by Everett and Meeuwig (*1975*) for soaking antelope bitterbrush seeds in hydrogen peroxide. We also soaked seeds from the same lots in water under similar conditions. Germination was compared for seeds in these treatments, for untreated control seeds, and for seeds soaked for 30 min in 3-percent aqueous solution of thiourea.

Soaking Temperature

To obtain a more precise estimate of the influence of temperature on the enhancement of germination by soaking with hydrogen peroxide, we tested germination of seeds soaked for 0.5 through 8 hours at 0°, 2°, 5°, 10°, 15°, 20°, 25°, and 30°C. Only the Reno seed source was used in this experiment. For temperature maintenance, seeds were soaked inside dark germinators and, because of the size of the germinators, the seeds were continuously stirred rather than shaken.

Concentrations of Hydrogen Peroxide

Seeds of antelope bitterbrush from the Reno source were soaked in 1-, 5-, 10-, 15-, and 30-percent aqueous solutions of hydrogen peroxide for 0.5, 1, 2, 4, 6, and 8 hours at 15°C in dark germinators. The soaking solutions were stirred continuously.

Temperature Profiles

Seeds from the Reno source were treated by the standard Everett and Meeuwig (*1975*) procedure (1-percent hydrogen peroxide with shaking) before incubation. The standard 55 constant and alternating temperature regimes were used for the germination profile.

Soaking Time and Temperature--Other Species

Seeds of desert bitterbrush and cliff rose, 3 months after harvest, were soaked in 1-, 5-, 10-, 15-, and 10-percent solutions of hydrogen peroxide for 0.5, 1, 2, 4, 6, and 8 hours at 15°C. Soaking was done in dark germinators with continous stirring. Seeds of desert bitterbrush were rubbed clean from the papery flower parts before soaking. Cliff rose seeds were soaked with the dried, funnel form flower parts persistent around the seeds. After soaking, the seeds were incubated at 15°C for 4 weeks.

Temperature Profiles

Standard 55 temperature regime profiles were conducted for both desert bitterbrush and cliff rose seeds. The seeds were pretreated by soaking for 6 hours in 1-percent hydrogen peroxide; the same procedure was used for antelope bitterbrush.

RESULTS

Control Profiles

For the 55 temperature regimes of the standard germination profile, seeds of antelope bitterbrush averaged only 16-percent germination, but this was significantly better (P=0.01) than the other two species (table 1). Germination was very low for the seeds of cliff rose and desert bitterbrush.

Table 1.--*Mean germination at 55 constant and alternating temperatures of antelope bitterbrush, desert bitterbrush, and cliff rose seeds without pretreatment*[1]

Species	Germination
	Percent
Antelope bitterbrush	16 a
Desert bitterbrush	3 c
Cliff rose	5 b

[1] Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Antelope Bitterbrush

Seeds of antelope bitterbrush germinated at a wide range of constant and alternating temperatures without pretreatment (table 2). Some germination occurred at 85 percent of the regimes tested (table 3). Optimum temperature regimes for germination were spread over a wide range of warm period temperatures from 15° to 30°C (table 2). Except for 10°/25°C (10°C for 16 hours/25°C for 16 hours in each 24-hour period) the optima occurred at 0° to 5°C night temperatures which, as we will see in a later section, are the ideal temperatures for stratification of antelope bitterbrush seeds. Essentially, during the 4-week incubation period, antelope bitterbrush seeds were partially self-stratifying themselves at these incubation temperatures. Partitioning the profiles into percentiles indicated that 51 percent of the regimes had germination between 10 and 25 percent and 27 percent had germination below 10 percent (table 3).

Desert Bitterbrush

The germination profile for desert bitterbrush seeds was considerably different with no evidence of self-stratification. There was no germination at 0°C or any temperature regime that alternated with 0°C (table 4). The optimum regimes were restricted to constant temperatures of 5° through 20°C except for 10°/15°C. Germination occurred at only 51 percent of the regimes tested, and an overwhelming 95 percent of the regimes had germination below 10 percent. Overall germination of desert bitterbrush without pretreatment was very low.

Cliff Rose

Germination of cliff rose seeds was low at all temperatures, and some germination occurred at only 60 percent of the temperatures tested. The optimum temperature regimes for germination were scattered over a wide range and accounted for 27 percent of the possible regimes (table 5). Some of the optima occurred in the self-stratifying range at 0°/25°, 2°/25°, 2°/30°, and 5°/20° through 5°/30°C, but others were the warm regimes of 20°/25° to 20°/30°C. On a percentile basis, 67 percent of the regimes had germination below 10 percent.

Table 2.--*Quadratic response surface for percent germination of antelope bitterbrush seeds without pretreatment before incubation* [1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	11±8	17±7	24±6	30±6	32±6	32±6	30±6	25±7	17±10
2		8±8	14±6	23±5	28±5	31±5	32±5	30±5	25±5	18±8
5			10±7	19±4	25±4	29±4	30±4	29±4	25±4	18±7
10				11±7	18±5	23±5	26±5	25±4	22±5	17±6
15					9±7	15±5	19±5	19±5	17±5	13±7
20						5±7	9±5	11±4	10±5	7±8
25							3±8	0	1±7	2±9
30								13±12	0	0
35									0	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Table 3.--*Comparison of parameters synthesized from quadratic response surfaces for germination profiles for antelope bitterbrush, desert bitterbrush, and cliff rose seeds without treatment before incubation*

Parameters	Cliff rose	Desert bitterbrush	Antelope bitterbrush
	Percent		
Regimes with some germination	60	51	87
Mean germination	9	5	19
Regimes with optimum germination	27	11	22
Mean of optima	13	8	30
Germination percentiles:			
< 10	67	95	27
10-25	33	5	51
26-50	0	0	22
51-75	0	0	0
76-90	0	0	0
> 90	0	0	0

Table 4.--*Quadratic response surface for percent germination of desert bitterbrush seeds without pretreatment before incubation* [1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	0	0	0	0	0	0	0	0	0
2		0	5 ±4	5 ±3	4 ±3	4 ±3	3 ±3	3 ±3	3 ±4	0
5			8 ±4	7 ±2	6 ±2	5 ±2	4 ±2	3 ±2	2 ±3	0
10				11 ±3	9 ±2	7 ±2	5 ±2	3 ±2	1 ±4	0
15					11 ±3	8 ±2	5 ±2	2 ±3	0	0
20						9 ±3	5 ±2	0	0	0
25							5 ±3	0	0	0
30								2 ±5	0	0
35									0	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Table 5.--*Quadratic response surface for percent germination of cliff rose seeds without pretreatment before incubation* [1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	0	0	0	0	0	12 ±5	0	3 ±5	0
2		0	0	0	0	0	13 ±4	12 ±3	5 ±4	0
5			0	0	8 ±5	13 ±4	14 ±3	13 ±3	8 ±3	1 ±6
10				2 ±7	7 ±4	13 ±3	15 ±3	15 ±3	11 ±3	4 ±5
15					4 ±5	11 ±3	15 ±3	15 ±3	12 ±3	6 ±5
20						7 ±4	12 ±3	13 ±3	12 ±4	0
25							8 ±4	10 ±3	0	0
30								5 ±4	6 ±3	3 ±5
35									0	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Thiourea

The maximum germination enhancement for all three species occurred with soaking the seeds for 30 min in a 3-percent solution of thiourea (tables 6, 7, 8). Germination enhancement, not statistically different (P=0.01) from the maximum, occurred at a relatively wide range of soaking times, up to 120 min, in a 3- or 5-percent concentration. This is a much longer soaking time than was originally proposed by Pearson (*1957*). He found that long-duration soaking inhibited germination. Antelope bitterbrush seeds have been shown to be sensitive to the temperature of the soaking solution with high soaking temperatures reducing subsequent germination (Neal and Sanderson *1975*). It may be that high soaking temperatures led Pearson to discount the value of longer duration thiourea treatments in enhancing germination. The value of longer duration soaking in thiourea solutions was originally pointed out by the late Eamor Nord (personal communication).

For the overall mean germination at the 55 constant and alternating temperature regimes tested, antelope bitterbrush seeds had significantly higher (P=0.01) germination than the other species (table 9). Cliff rose seeds were intermediate in germination, and desert bitterbrush germination profiles had the lowest average germination.

Table 6.--*Percent germination of antelope bitterbrush seeds soaked in 0- to 5-percent concentrations of thiourea for 1 through 120 min at 15°C. Subsequent incubation at 15°C for 4 weeks*[1]

Thiourea concentration (percent)	Germination for the following soaking times, in minutes						
	1	5	10	15	30	60	120
	Percent						
0	9g	10fg	8g	12fg	8g	10e-g	10e-g
.5	10e-g	9g	6g	8g	10fg	12fg	8g
1	16e-g	12fg	8g	12fg	24d-g	16e-g	20e-g
3	44a-d	40a-d	46a-c	54ab	57a	40a-d	26c-g
5	30c-f	28c-g	20e-g	24d-g	26c-g	34b-e	50c-f

[1] Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 7.--*Percent germination of desert bitterbrush seeds soaked in 0- to 5-percent concentrations of thiourea for 1 through 12 min at 15°C. Subsequent incubation at 15°C for 4 weeks*[1]

Thiourea concentration (percent)	Germination for the following soaking times, in minutes						
	1	5	10	15	30	60	120
	Percent						
0	11d	12b-d	9d	15a-d	10cd	12b-d	10cd
.5	12b-d	10cd	10cd	12b-d	14b-d	12b-d	12b-d
1	10cd	12b-d	10cd	14b-d	12b-d	16a-d	14b-d
3	18a-b	25a-d	30a-c	32ad	35a	30a-c	26a-d
5	24a-d	20a-d	18a-d	20a-d	15a-d	20a-d	10c-d

[1] Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 8.--*Percent germination of cliff rose seeds soaked in 0- to 5-percent concentrations of thiourea for 1 through 120 min at 15°C. Subsequent incubation at 15°C for 4 weeks*[1]

Thiourea concentration (percent)	Germination for the following soaking times, in minutes						
	1	5	10	15	30	60	120
	Percent						
0	3e	5de	8de	10c-e	6de	8de	8de
.5	6de	8de	6de	8de	10c-e	8de	8de
1	10c-e	16b-e	18b-e	18b-e	20b-d	24b-d	8b-e
3	24b-d	28a-c	24b-d	36ab	49a	32ab	24b-d
5	32ab	30a-c	24b-d	18b-e	20b-d	20b-d	16b-e

[1] Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 9.--*Mean germination of antelope bitterbrush, desert bitterbrush, and cliff rose seeds soaked in a 3-percent thiourea solution for 30 min before incubation at 55 constant and alternating temperatures*[1]

Species	Germination
	Percent
Antelope bitterbrush	43 a
Desert bitterbrush	21 c
Cliff rose	34 b

[1] Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Antelope Bitterbrush

Seeds of antelope bitterbrush germinated at all temperatures tested except 0°/0°, 35°/40°, and 40°/40°C after being treated with thiourea (table 10). The mean germination of regimes with some germination was 46 percent (table 12).

Table 10.--*Quadratic response surface for percent germination of antelope bitterbrush seeds soaked in a 3-percent solution of thiourea for 30 min before incubation*[1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	50±10	55±8	60±6	61±7	59±7	53±7	43±7	29±8	12±11
2		51±9	56±7	<u>62±5</u>	<u>64±5</u>	<u>63±6</u>	57±6	48±5	36±6	19±9
5			57±8	<u>64±5</u>	<u>67±4</u>	<u>66±5</u>	<u>62±5</u>	54±5	43±5	28±8
10				<u>60±7</u>	<u>65±5</u>	<u>67±5</u>	<u>65±5</u>	59±5	49±5	36±7
15					<u>57±8</u>	<u>60±6</u>	<u>60±5</u>	56±5	48±6	37±8
20						47±8	48±6	46±5	41±6	31±8
25							30±8	30±5	26±6	18±8
30								6±9	4±8	1±10
35									25±13	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Table 11.--*Quadratic response surface for percent germination of desert bitterbrush seeds soaked in a 3-percent solution of thiourea for 30 min before incubation*

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	13±8	3±7	10±6	19±6	24±6	24±6	20±6	11±7	2±11
2		9±8	1±6	15±5	24±5	29±5	30±5	26±5	18±6	0
5			5±7	20±4	30±4	36±4	37±4	34±4	26±5	14±8
10				24±7	35±5	42±5	44±5	42±5	35±6	0
15					35±7	42±5	46±5	45±5	39±6	39±9
20						38±7	42±5	42±5	37±7	0
25							33±7	34±6	30±7	0
30								20±10	18±10	0
35									0	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Optimum temperature regimes for germination occurred at 18 percent of the temperatures tested with an average germination of 65 percent. The optima occurred at temperatures from 10° to 25°C alternating with 2° to 10°C. Based on a percentile breakdown, 49 percent of the regimes produced germination between 51 and 75 percent, and only 11 percent had germination below 10 percent.

Desert Bitterbrush

Seeds of desert bitterbrush germinated at 85 percent of the temperature regimes tested after treatment with thiourea (table 11). Besides 0°/0°C, desert bitterbrush seeds failed to germinate at 35°/35° or 40°/40°C and most of the temperature regimes that alternated with 40°C (table 12). Optimum regimes for germination were clustered around 15°/25°C and accounted for 15 percent of all regimes, with a mean germination of 43 percent. Based on percentiles, 47 percent of the temperature regimes produced germination between 26 and 50 percent. More than a quarter of the regimes had germination below 10 percent.

Cliff Rose

After treatment with thiourea, cliff rose seeds germinated at 93 percent of the temperatue regimes tested (table 12). Only the very cold and extremely warm regimes failed to support some germination (table 13). Optima constituted 16 percent of the regimes in a tight cluster in the 20° and 25°C warm period temperatures, alternating with 2° to 15°C cold period temperatures. The mean germination at the optimum regimes was 66 percent. Based on percentiles, 29 percent of the regimes produced germination between 51 and 75 percent, and 15 percent had germination below 10 percent.

Table 12.--*Comparison of parameters synthesized from quadratic response surfaces for germination profiles for antelope bitterbrush, desert bitterbrush, and cliff rose seeds soaked in a 3-percent solution of thiourea for 30 min before incubation*

Parameters	Cliff rose	Desert bitterbrush	Antelope bitterbrush
	----------*Percent*----------		
Regimes with some germination	93	85	95
Mean germination	38	26	46
Regimes with optimum germination	16	15	18
Mean of optima	66	43	65
Germination percentiles:			
< 10	15	26	11
10-25	18	27	7
26-50	38	47	33
51-75	29	0	49
76-90	0	0	0
> 90	0	0	0

Table 13.--*Quadratic response surface for percent germination of cliff rose seeds soaked in a 3-percent solution of thiourea for 30 min before incubation*[1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 18 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	0	18±11	36±9	48±8	53±9	53±8	46±8	34±9	15±14
2		8±13	21±10	39±7	51±7	57±7	57±7	50±7	38±8	20±12
5			24±11	42±6	54±6	60±6	60±6	54±6	42±6	25±10
10				42±9	54±7	61±6	62±6	57±6	45±6	28±9
15					49±10	56±7	57±7	53±7	42±7	25±10
20						45±10	47±7	43±6	33±7	17±10
25							31±10	27±7	18±7	2±10
30								6±11	3±10	18±12
35									30±16	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Stratification--Temperature and Duration

Stratification at -2° or -4°C was not effective in enhancing the germination of antelope and desert bitterbrush and cliff rose (fig. 1). We show data for -4°C only, but the results for -2°C were similar for all three species. Stratification at 0°C was effective in enhancing the germination of all three species (fig. 2).

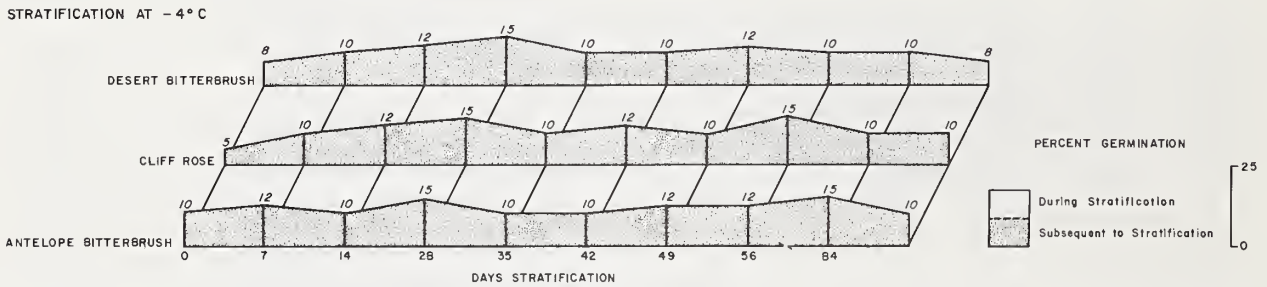

Figure 1.--Germination of antelope and desert bitterbrush and cliff rose seeds during and subsequent to 7 through 84 days stratification at -4°C. Poststratification incubation at 15°C for 4 weeks.

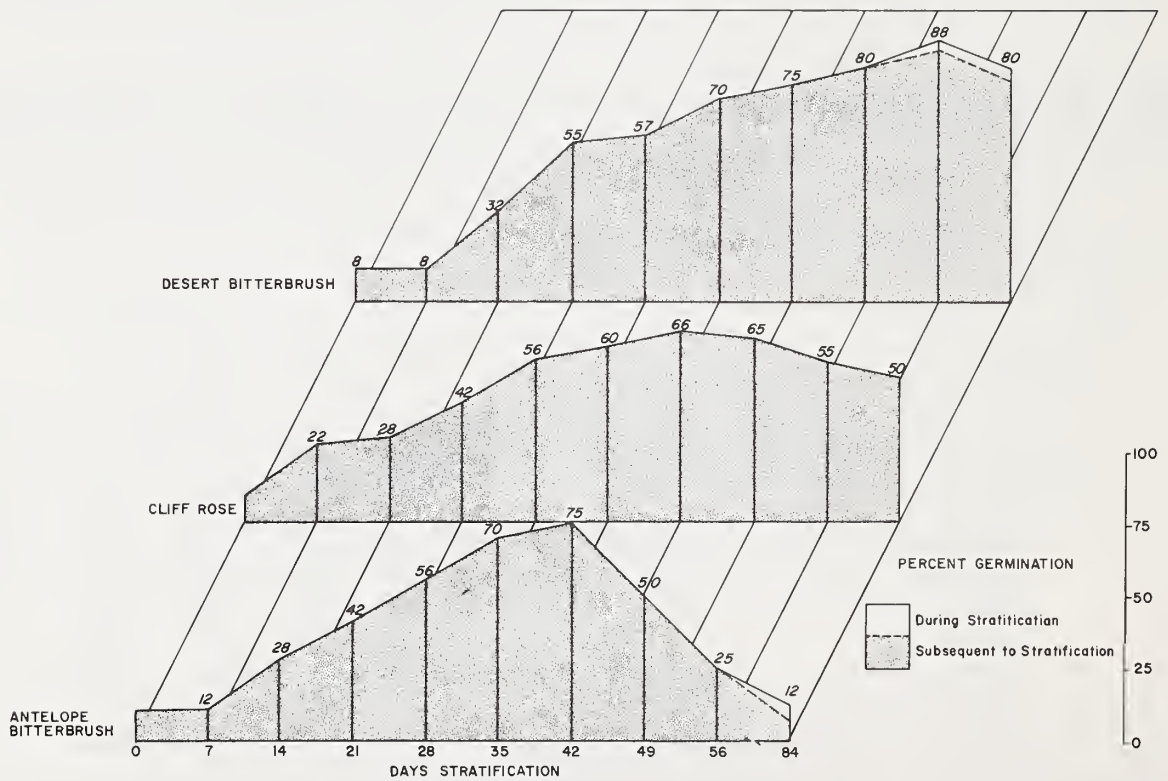

Figure 2.--Germination of antelope and desert bitterbrush and cliff rose seeds during and subsequent to 7 through 84 days stratification at 0°C. Poststratification incubation at 15°C for 4 weeks.

Peak germination enhancement of antelope bitterbrush occurred after 6 weeks stratification. Stratification longer than 6 weeks resulted in a drop in subsequent germination. With 8 weeks stratification, a few germinated seeds were found in the stratification plates. The peak enhancement of cliff rose seeds also occurred at 6 weeks stratification, but the drop in germination at 12 weeks was only 16 percent below the peak compared with 63 percent lower with antelope bitterbrush. Cliff rose seeds did not germinate in the stratification plates at 0°C. The peak in germination enhancement of desert bitterbrush seeds occurred after 8 weeks stratification at 0°C. There was a slight drop in germination with 12 weeks stratification. Some germination occurred in the stratification plates at end after 7 weeks stratification. Although the peak in germination enhancement occurred later with desert bitterbrush compared with the other species, initial enhancement after 3 weeks stratification was also greater than for the other species.

Raising the stratification temperature to 2°C greatly shortened the stratification period required for peak germination enhancement for antelope bitterbrush seeds (fig. 3). The peak in germination enhancement occurred after only 3 weeks stratification. After 5 weeks stratification at 2°C, subsequent germination declined. After 3 weeks stratification, some seeds of antelope bitterbrush were germinated in the stratification plates, and by 12 weeks stratification, 82 percent of the germinable seeds were germinated in the stratification plates. The peak germination enhancement of cliff rose seeds occurred after 6 weeks stratification at 2°C, the same time required at 0°C. From 1 through 6 weeks, the enhancement of germination was similar for both temperatures except subsequent germination after stratification at 2°C was 10 to 20 percent higher than for the same duration at 0°C. After 6 weeks stratification, the germination of cliff rose seeds dropped sharply until at 12 weeks it was less than 20 percent of the maximum. After 7 weeks stratification, some germinated seeds were found in the stratification plates. The subsequent germination of desert bitterbrush seeds was optimumly enhanced by 5 and 7 weeks stratification at 2°C. After 7 weeks, germination declined rapidly. Germinated seeds were found in the stratification plates after 6 weeks.

Increasing the stratification temperature to 5°C further reduced the required time for stratification (fig. 4) for all species. The peak enhancement for antelope bitterbrush seeds occurred after 2 weeks stratification with a rapid decline in germination with further stratification. Germinated seeds were found in the stratification plates after 2 weeks. The germination of cliff rose and desert bitterbrush seeds was enhanced to near optimum levels after 1 week of stratification at 5°C and remained high for 5 weeks. After 5 weeks stratification , germination declined rapidly.

When the stratification temperature was increased to 8° or 10°C (we only show 10°C), germination was not enhanced for any of the three browse species (fig. 5). Prolonged stratification at these temperatures lead to decay and total loss of germinability.

Apparently, antelope and desert bitterbrush and cliff rose seeds with stratification requirements satisfied are susceptible to pathogens. We noted that prolonged stratification leads to liquefication of the contents of the seed.

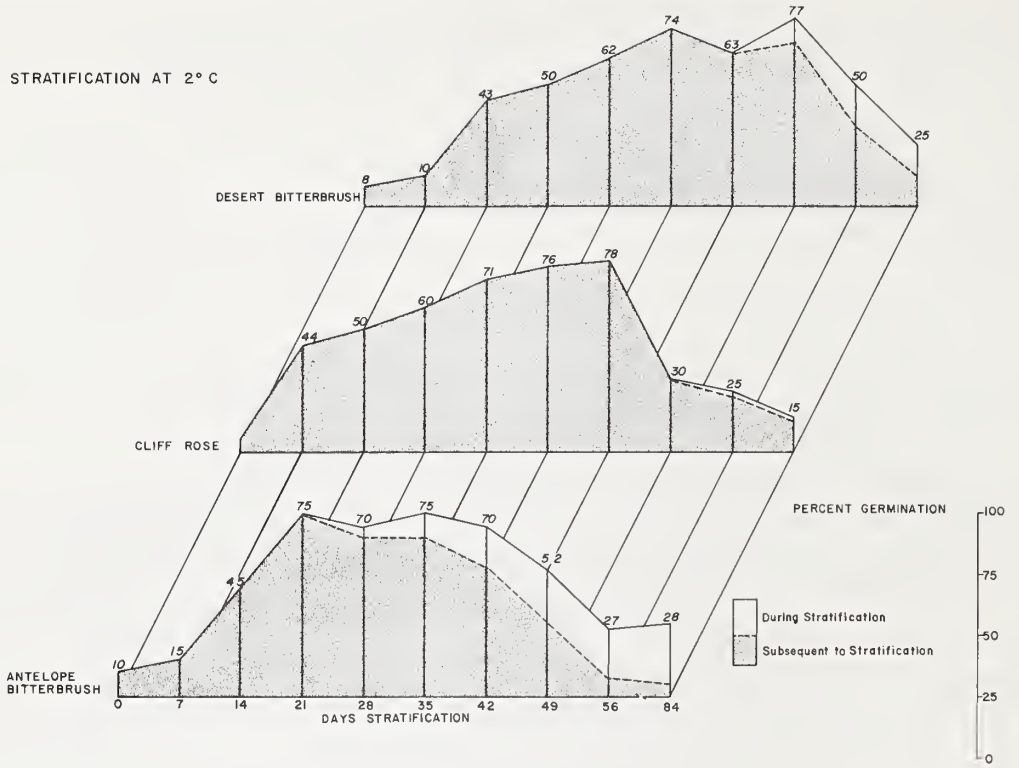

Figure 3.--Germination of antelope and desert bitterbrush and cliff rose seeds during and subsequent to 7 through 84 days stratification at 2°C. Post-stratification incubation at 15°C for 4 weeks.

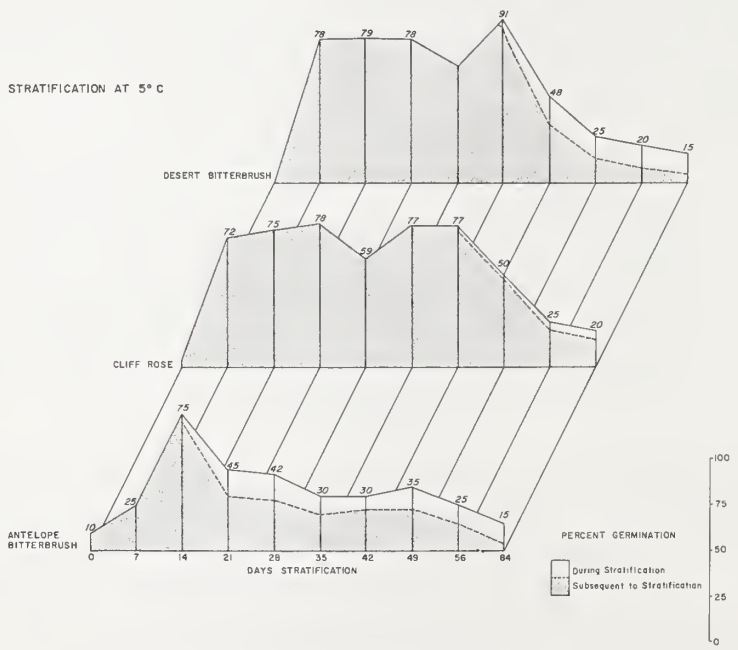

Figure 4.--Germination of antelope and desert bitterbrush and cliff rose seeds during and subsequent to 7 through 84 days strtification at 5°C. Poststra-tification incubation at 15°C for 4 weeks.

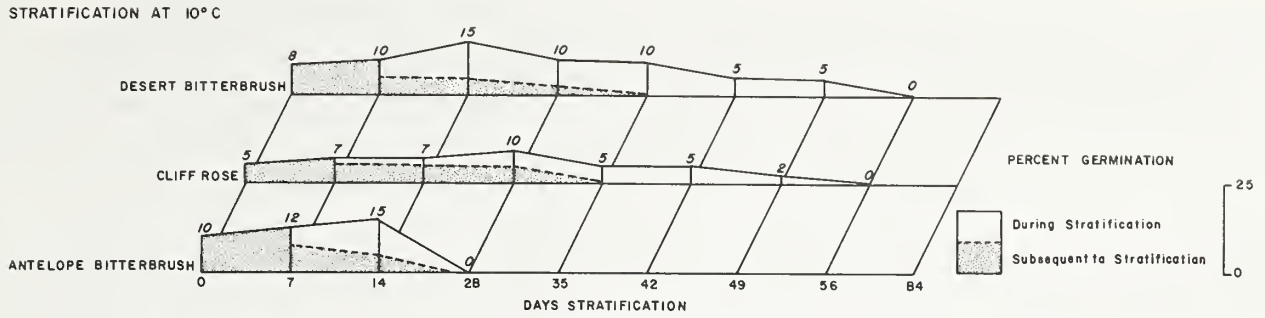

Figure 5.--Germination of antelope and desert bitterbrush and cliff rose seeds during and subsequent to 7 through 84 days stratification at 10°C. Post-stratification incubation at 15°C for 4 weeks.

Sometimes, the seeds become covered with fungal mycelia, but they are not always present. Antelope bitterbrush seeds appear most susceptible and cliff rose seeds most resistant to fungus attack.

The usual recommended stratification for antelope bitterbrush is 2 to 3 months (U.S. Department of Agriculture, Forest Service *1948*). Petzold (as cited by Deitschman et al. *1974*) found that short stratification periods of as little as 2 weeks gave adequate germination.

Stratification of bitterbrush is intricately related to temperature and time. Hormay (*1943*) reported that the stratification requirements for bitterbrush seeds were 5 to 8 weeks at 0° to 5°C. This temperature range is supported by our investigation, but our results indicate that the duration can be shortened. More importantly, excessively long stratification can reduce subsequent germination.

Osmotic Stress

Lowered osmotic potentials significantly affected (P=0.01) stratification effectiveness and subsequent germination of bitterbrush (table 14). This may have resulted from reduced oxygen (O_2) availability in the osmotic solution, although polyethylene glycol is relatively stable when exposed to air. Rarely would antelope bitterbrush seeds be planted in soils where low osmotic potentials would be a problem, but they may be a limiting factor in the range of the species. More importantly, lowered germination by osmotic stress may be symptomatic of the influence of many forms of stress on the stratification process.

Matric Potential

Moist sand was an excellent stratification material that produced subsequent germination of antelope bitterbrush seeds comparable to that obtained with moist germination paper (table 15). Slightly dry (-4 bars) sand was not a satisfactory stratification material. Clay, with its greater waterholding capacity, provided a marginal stratification environment at -4 bars, but was unsatisfactory at lower matric potentials.

Table 14.--*Percent germination of antelope bitterbrush seeds with 4 weeks incubation at 15°C after stratification in sand or clay at 0 to -12 bars matric potential at 2° or 5°C for 10 to 14 days*[1]

Temperature (°C)	Duration	Matric potential (bars)										Non-stratified seed
		Sand					Clay					
		0	-4	-6	-8	-12	0	-4	-6	-8	-12	
	Days	*Percent*										
2	10	48cd	20gh	14h	16 h	20gh	44cd	38de	22gh	18gh	16h	22gh
	14	72ab	14h	18gh	20gh	18gh	70ab	62bc	16h	20gh	24f-h	22gh
5	10	52cd	16h	20gh	12h	24f-h	52cd	42de	32e-g	24	21gh	22gh
	14	76ab	18gh	24f-h	18gh	20gh	8a	70ab	22gh	12h	25f-h	22gh

[1] Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 15.--*Percent germination of antelope bitterbrush seeds with 4 weeks incubation at 15°C after stratification with 0 to -12 bars osmotic potential at 2° or 5°C for 10 or 14 days*[1]

Temperature (°C)	Duration	Osmotic potential (bars)					Non-stratified seed
		0	-4	-6	-8	-12	
	Days	*Percent*					
2	10	52 c	10 d-h	0 h	12 d-h	0 h	22 d
	14	68 ab	16 d-g	8 d-h	10 d-h	4 e-h	22 d
5	10	56 bc	20 d-f	6 e-h	6 e-h	10 d-h	22 d
	14	80 a	12 d-h	16 d-g	18 d-f	2 gh	22 d

[1] Means followed by the same letter are not significantly different at the 0.01 level of probability, as determined by Duncan's multiple range test.

Mode of Action of Stratification

No one knows for certain what is the mode of action for stratification enhancing seed germination; however, we (Young and Evans *1976*) previously suggested a possibility based on the research of the French seed physiologist, Come (*1967*).

Embryos require very little O_2 in the environment to germinate. The lower the temperature, the less O_2 is needed (Come and Tissaoui *1972*). After imbibition, the embryo receives dissolved O_2 from the water imbibed by the seedcoat; however, the seedcoat of many species of Rosaceae contains phenolic constituents that fix part of the dissolved O_2 by oxidation and lower the quantity available to the embryo for other purposes (Come *1967*). The higher the temperature, the greater the O_2 requirement of the embryo, but the quantity of available O_2 decreases because at higher temperatures it is less soluble and phenolic substances fix more of it. At 2°C, about 14 p/m O_2 are soluble in water, but only 10 p/m are soluble at 15°C (Streeter *1935*). Because low temperatures increase solubility of O_2 in water and reduce both the requirements for it and the fixing capability of the seedcoat, stratification enhances germination of antelope bitterbrush seeds.

Stratification in the Field

These results suggest that an ideal field stratification environment for these species would be one with constant moisture near field capacity and a temperature regime of 0° to 5°C. A continous midwinter snow cover may create such an environment (Nord *1965*). Unfortunately, many critical winter ranges for big-game animals are located at elevations with intermittent snow cover, in which soil moisture may not be continously at optimum levels. Seedbed temperature may be above 5°C or below 0°C.

Land managers probably are taking a large risk by spring seeding non-thiourea-treated seeds of these species. If conditions are optimum in the seedbed, stratification requirements can be satisfied in as little as 1 to 2 weeks; however, any departure from optimum temperature and moisture regimes will prolong the required duration of stratification or negate the effect of stratification.

Mean germination of desert bitterbrush at 55 constant and alternating temperatures after 2 weeks stratification at 5°C was significantly higher (P=0.01) than that for the other species (table 16). The mean germination of cliff rose seeds was intermediate and that for antelope bitterbrush seeds was lowest in average germination at this wide range of constant and alternating temperatures.

Antelope Bitterbrush

The quadratic response surface for antelope bitterbrush germination reveals some germination at 91 percent of the temperature regimes tested (tables 17 and 18). The optimum temperatures regimes for germination were loosely clustered around 5°/15°C encompassing 23 percent of the temperature regimes with an average germination of 52 percent. Partitioning the profile into percentiles shows

Table 16.--*Mean germination of antelope bitterbrush, desert bitterbrush, and cliff rose seeds with cool, moist stratification before incubation at 55 constant and alternating temperatures* [1]

Species	Germination
	Percent
Antelope bitterbrush	31 c
Desert bitterbrush	38 a
Cliff rose	34 b

1 Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 17.--*Quadratic response surface for percent germination of antelope bitterbrush seeds stratified for 2 weeks at 5°C* [1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	38±10	43±8	48±7	51±7	50±7	46±7	34±7	30±8	17±11
2		40±10	44±7	50±5	52±6	52±6	48±6	51±5	32±6	19±10
5			46±8	51±5	54±5	53±5	50±5	43±5	33±5	20±8
10				50±8	53±6	52±5	48±5	42±5	32±6	19±8
15					47±9	46±6	43±6	36±6	27±6	14±8
20						36±8	33±6	26±5	17±6	4±9
25							18±9	12±7	2±7	11±10
30								8±12	17±11	0
35									0	0
40										0

1 Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

that 52 percent of the temperature regimes produced germination from 26 to 50 percent (table 18). Only 15 percent of the regimes produced germination greater than 50 percent. On the other end of the germination spectrum, 15 percent of the regimes produced germination of less than 10 percent.

Desert Bitterbrush

The quadratic response surface for germination of seeds of desert bitterbrush showed a lower number of temperature regimes that supported some germina-

tion than antelope bitterbrush, but a higher average germination (tables 18 and 19). Desert bitterbrush seeds failed to germinate at 40°C or colder tempera-

Table 18.--*Comparison of parameters synthesized from quadratic response surfaces of germination profiles for antelope bitterbrush, desert bitterbrush, and cliff rose seeds after cool, moist stratification*

Parameters	Cliff rose	Desert bitterbrush	Antelope bitterbrush
Regimes with some germination	96	80	91
Mean germination	37	50	36
Regimes with optimum germination	15	11	23
Mean of optima	55	72	52
Germination percentiles:			
<10	11	22	15
10-25	16	9	18
26-50	51	37	52
51-75	22	31	15
76-90	0	2	0
>90	0	0	0

Table 19.--*Quadratic response surface for percent germination of desert bitterbrush seeds stratified for 2 weeks at 5°C*[1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	34±12	38±10	43±9	45±9	43±9	37±9	38±10	15±15	0
2		42±12	46±9	51±7	52±7	50±8	44±7	34±8	21±12	0
5			57±10	61±6	61±6	58±7	52±6	42±6	28±9	0
10				72±10	72±7	68±7	61±7	50±7	36±9	0
15					77±11	72±8	64±7	52±7	37±9	18±14
20						71±11	61±7	49±7	33±10	0
25							53±11	40±8	23±11	0
30								25±15	7±15	0
35									0	0
40										0

[1]Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

tures alternating with 40°C except for 15°/40°C. Optimum temperature regimes were tightly clustered at 10°/10°, 10°/15°, 10°/20°, 15°/15°, 15°/20°, and 20°/20°C. The mean of the optima was 72 percent. Partitioned into percentiles, 68 percent of the temperature regimes supported germination between 26 and 75 percent. The failure to germinate at most 40°C temperatures was reflected in the 22 percent of the regimes that produced germination below 10 percent.

Cliff Rose

Seeds of cliff rose had some germination at all temperature regimes except 0°/0° or 0°/2°C (table 20). The mean germination of the 52 regimes that produced some germination was 37 percent (table 18). The temperature regimes that produced optimum germination were clustered around 5°/25°C and extended to 2°/25°C. The mean of the optima was 55 percent. On a percentile basis, 51 percent of the temperature regimes produced germination in the 26- to 50-percent range and only 11 percent were below 10 percent.

Hydrogen Peroxide

Initial Experiment--Antelope Bitterbrush

The extent to which soaking in hydrogen peroxide (H_2O_2) enhanced germination of antelope bitterbrush seeds depended on the source of seed (table 21). For seeds collected near Reno, our results indicated that H_2O_2 enhancement equaled that of thiourea and essentially duplicated results reported by Everett and Meeuwig (*1975*). For seeds from the other four sources, the H_2O_2 treatment

Table 20.--*Quadratic response surface for percent germination of cliff rose seeds stratified for 2 weeks at 5°C*[1]

Cold period temperature (°C) 16 hours	Estimated precent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	0	14±8	32±7	44±7	50±7	50±7	45±7	34±8	17±12
2		2±10	16±8	34±6	46±6	52±6	53±6	48±6	37±7	20±10
5			18±8	36±5	48±5	55±5	56±5	51±5	40±5	24±8
10				36±8	49±5	56±5	58±5	53±5	43±5	27±8
15					47±8	55±6	56±5	52±5	42±6	27±8
20						44±9	51±5	48±5	38±6	23±9
25							43±8	40±6	31±6	16±8
30								28±8	20±6	5±8
35									5±10	9±10
40										26±14

1 Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Table 21.--*Percent germination by source of antelope bitterbrush seeds soaked and shaken in a 1-percent solution of hydrogen peroxide or in water; dry control seeds and seeds were soaked in a 1-percent thiourea solution*[1]

Soak solution	Time	Germination[2] of seeds from				
		Boise	Reno	Ada County	Twin Falls	Jiggs
	Hours	*Percent*				
Hydrogen peroxide (1 percent)	1	15 c-e	10 c	25 b-d	29 b	45 b-d
	2	31 bc	41 b	39 b	19 bc	46 bc
	3	23 b-e	49 b	30 bc	38 b	46 bc
	4	27 b-d	56 ab	24 b-d	33 b	57 b
	5	38 b	76 a	19 b-d	22 bc	45 bc
Water	1	2 e	5 c	5 d	4 c	18 de
	5	8 de	6 c	12 cd	2 c	29 cd
None (dry)	0	2 e	4 c	6 d	1 c	7 e
Thiourea (3 percent) for 30 min	0	87 a	64 a	77 a	73 a	78 a

[1]After soaking, seeds were incubated at 15°C for 4 weeks.

[2]In each column, means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

markedly increased germination, in comparison with the germination of untreated seeds; however, for each of these sources, the enhancement of germination was significantly less (P=0.01) with H_2O_2 treatment than with thiourea treatment.

Germination response to soaking time varied by source of seed (table 21). Again, the time response of seeds from Reno approximated that reported by Everett and Meeuwig (*1975*). For seeds from Jiggs, Nev., percentage germination was six times higher in seeds for 1 hour in the H_2O_2 solution than in dry seeds, but additional soaking did not improve germination. Seeds from this source also had a markedly increased percentage of germination, compared with seeds of the control, after soaking in water for 5 hours. In this experiment and in all others, the seeds that germinated after treatment with H_2O_2 had clear seedcoats with no trace of the normal dark pigmentation.

Soaking Temperature

The temperature of the soaking solution did not greatly influence subsequent germination of seeds from Reno as long as it did not exceed 15°C (table 22). Percentage germination of seeds soaked for 4 hours at 0°C was not significantly different from that of seeds soaked for 4 hours at 15°C. When seeds were soaked for 6 hours (intermediate time periods not shown), the most effective soak temperature was 10°C rather than 15°C.

Table 22.--*Influence of time and temperature of soaking in 1-percent hydrogen peroxide solution on percent germination of antelope bitterbrush seeds*[1]

Soaking temperature (°C)	Percent germination[2] of seeds soaked for indicated time (hours)			
	0.5	1	4	6
	Percent			
0	2 j	28 e-g	51 a-c	46 b-d
2	7 h-j	29 d-f	46 b-d	50 a-c
5	6 ij	29 d-f	53 a-c	42 b-d
10	9 g-i	20 e-j	56 ab	48 b-d
15	4 j	26 e-h	68 a	28 e-g
20	7 h-j	21 e-j	35 c-e	0 j
25	3 j	11 g-j	29 d-f	3 j
30	4 j	15 g-j	24 e-i	0 j

[1]Seeds were soaked in the dark and then incubated at 15°C for 4 weeks.
[2]Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Concentration of Hydrogen Peroxide

Concentration of H_2O_2 greater than 1 percent enhanced germination of antelope bitterbrush seeds in shorter soaking times (table 23). The same germination that required 6 hours soaking in a 1-percent solution could be obtained in 1 hour with a 5-percent solution. At concentrations greater than 5 percent, germination was depressed by prolonged soaking. With 30-percent H_2O_2, soaking for longer than 30 min depressed germination.

Note: Hydrogen peroxide is a very reactive chemical. At concentrations greater than 3 percent, it can cause severe burns to exposed skin.

Soaking Time and Concentration--Desert Bitterbrush

Soaking desert bitterbrush seeds for 6 hours in 1-percent H_2O_2 enhanced germination, but not so it was clearly significantly different ($P=0.01$) from the control (table 24). As with antelope bitterbrush seeds, shorter soaking times at higher concentrations also enhanced germination. At the higher concentrations of H_2O_2, prolonged soaking resulted in reduced or complete inhibition of germination.

Soaking Time and Concentration--Cliff Rose

Germination of cliff rose was not significantly enhanced by soaking in H_2O_2 at the 0.01 level but was at the 0.05 level of significance (table 25). Gener-

ally, there was very little enhancement of cliff rose germination with hydrogen peroxide soaking.

Table 23.--*Influence of concentration of hydrogen peroxide and soaking time on the subsequent percent germination of antelope bitterbrush seeds from the Reno, Nev., source*[1]

Soaking time (hours)	Percent germination of seeds for indicated hydrogen peroxide concentrations (percent)				
	1	5	10	15	30
	Percent				
0.5	4 e	21 b-e	38 ab	30 ad	36 a-c
1	16 b-e	36 bc	40 a	36 bc	16 c-e
2	34 a-c	30 a-d	36 a-c	28 a-d	18 b-e
4	27 a-d	34 a-c	34 a-c	21 b-e	4 e
6	36 a-c	34 a-c	36 a-c	12 de	0 e
8	32 a-d	30 a-d	12 de	4 e	2 e
Control	5 e				

[1]Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 24.--*Influence of concentration of hydrogen peroxide and soaking time on the subsequent percent germination of desert bitterbrush seeds*[1]

Soaking time (hours)	Percent germination of seeds for indicated hydrogen peroxide concentrations (percent)				
	1	5	10	15	30
	Percent				
0.5	10 a-d	30 a	22 a-d	2 d	4 cd
1	12 a-d	21 a-d	18 a-d	6 cd	0 d
2	28 ab	24 a-c	24 a-c	4 cd	0 d
4	24 a-c	24 a-c	18 a-d	2 d	0 d
6	30 a	18 a-d	10 a-d	0 d	0 d
8	24 a-c	6 c-d	8 b-d	0 d	0 d
Control	11 a-d				

[1]Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 25.--*Influence of concentration of hydrogen peroxide and soaking time on the subsequent percent germination of cliff rose seeds*[1]

Soaking time (hours)	Percent germination of seeds for indicated hydrogen peroxide concentrations (percent)				
	1	5	10	15	30
	Percent				
0.5	22 a	20 ab	16 a-c	12 a-d	8 c-e
1	20 ab	18 a-c	10 b-e	8 c-e	0 e
2	18 a-c	16 a-c	8 c-e	10 b-e	0 e
4	22 a	20 ab	14 a-d	4 de	0 e
6	22 a	10 b-e	4 de	0 e	0 e
8	11 b-d	16 a-c	2 e	0 e	0 e
Control	4 de				

[1] Means followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's multiple range test.

Germination Profiles

The overall mean germination of antelope seeds, pretreated with 1-percent H_2O_2 for 6 hours was significantly higher (P=0.01) than that for the other two species (table 26). Desert bitterbrush seeds had intermediate germination, and the mean germination of cliff rose seeds was significantly lower.

Table 26.--*Mean germination of antelope bitterbrush, desert bitterbrush, and cliff rose seeds pretreated by soaking in a 1-percent aqueous solution of hydrogen peroxide for 6 hours before incubation at 55 constant and alternating temperatures* [1]

Species	Germination
	Percent
Antelope bitterbrush	21 a
Desert bitterbrush	19 b
Cliff rose	9 c

[1] Means followed by the same letter are not a significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Antelope Bitterbrush

The quadratic response surface for percent germination of H_2O_2 treated seeds reveals some germination at 85 percent of the temperature regimes tested with a mean germination of 26 percent (table 27). The optimum temperatures for germination clustered around 10°/10°, 10°/15°, and 10°/20°C with a mean of 49 percent. Dividing the profile into percentiles resulted in 47 percent of the profiles having germination from 26 to 50 percent. A large proportion of regimes, 29 percent, support germination only from 0 to less than 10 percent.

Desert Bitterbrush

The quadratic response surface for percent germination of desert bitterbrush seeds treated with H_2O_2 was similar to that of antelope bitterbrush (table 29). Some germination occurred at 87 percent of the 55 temperature regimes tested (tables 28 and 29). Mean germination of the regimes with some germination was 13 percent. The number of regimes with optimum germination was 13 percent of the total, the same as for antelope bitterbrush. The mean of the optima was 39 percent. The optimum regimes were clustered around 10°/20°, 10°/25°, and 10°/30°C or slightly higher warm period temperatures than for antelope bitterbrush. The percentile distribution of germination and temperature regimes for desert bitterbrush germination was practically identical to those for antelope bitterbrush seeds.

Cliff Rose

The quadratic response surface for percent germination of cliff rose seeds treated with H_2O_2 reveals a limited germination response (table 30). Germination occurred at 62 percent of the temperatures tested with a mean of 14 percent (table 28). The optimum temperature regimes for germination spread over a relatively wide range of temperatures (20 percent of the total) from 10°/10° through 20°/25°C. The lack of germination enhancement of cliff rose seeds with H_2O_2 treatments is illustrated by the 62 percent of the temperature regimes with less than 10-percent germination.

Frequency of Optima

The large number of germination-temperature profiles that were developed for this plant material gives us an opportunity to evaluate the frequency that given temperature regimes support optimum germination.

Antelope Bitterbrush

Optimum regimes for germination of antelope bitterbrush occurred at 36 percent of the 55 temperatures tested in at least one of the four treatments (table 31). Only one temperature, 5°/20°C, was always optimum. Most of the optimum temperatures, 70 percent, were in the self-stratifying zone of 5°C or less during the cold period. Among the treatments, there are shifts in optima around 5°/20°C, but few clear patterns. The optimum regimes for the control occurred at the most widely fluctuating regimes.

Table 27.--*Quadratic response surface for percent germination of antelope bitterbrush seeds soaked for 6 hours in 1-percent hydrogen peroxide*[1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	13±8	19±6	27±5	32±5	32±5	29±5	22±5	12±6	3±8
2		18±7	24±5	32±4	36±4	37±4	33±4	26±4	16±5	1±7
5			30±6	38±4	42±4	42±4	38±4	31±4	20±4	5±6
10				42±6	45±5	45±4	41±4	33±4	22±4	7±6
15					43±7	42±5	38±4	30±4	18±5	3±7
20						34±6	29±4	20±4	8±6	8±8
25							13±7	5±6	0	0
30								0	0	0
35									0	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Table 28.--*Comparison of parameters synthesized from quadratic response surfaces of germination profiles for antelope bitterbrush, desert bitterbrush, and cliff rose seeds treated with hydrogen peroxide*

Parameters	Cliff rose	Desert bitterbrush	Antelope bitterbrush
	Percent		
Regimes with some germination	62	87	85
Mean germination	14	23	26
Regimes with optimum germination	20	13	15
Mean of optima	25	37	49
Germination percentiles:			
<10	62	27	29
11-25	31	31	24
26-50	7	42	47
51-75	0	0	0
76-90	0	0	0
>91	0	0	0

Table 29.--*Quadratic response surface for percent germination of desert bitterbrush seeds soaked for 6 hours in 1-percent hydrogen peroxide* [1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	1±6	11±8	12±5	21±5	26±6	26±5	21±5	13±6	1±9
2		2±6	9±8	15±4	25±4	30±5	30±5	26±4	18±5	5±8
5			4±6	19±4	29±4	34±4	35±4	32±4	24±4	11±7
10				21±6	31±4	38±4	39±4	37±4	30±5	21±8
15					29±7	36±5	39±4	38±5	31±6	0
20						31±7	34±5	33±4	28±6	0
25							25±6	25±5	20±6	0
30								11±7	8±7	0
35									10±11	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Table 30.--*Quadratic response surface for percent germination of cliff rose seeds soaked for 6 hours in 1-percent hydrogen peroxide solution* [1]

Cold period temperature (°C) 16 hours	Estimated percent germination and confidence interval									
	Warm period temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0	0	0	0	0	0	4±7	3±7	0	0	0
2		0	1±13	6±8	9±6	10±6	9±6	6±6	0	0
5			0	0	17±5	18±5	17±5	13±5	8±7	1±12
10				23±9	25±6	26±5	24±5	21±5	16±6	8±10
15					28±8	28±6	26±5	22±6	17±7	0
20						25±8	23±5	19±6	13±8	0
25							14±8	9±6	0	0
30								5±11	12±12	0
35									0	0
40										0

[1] Means not lower than the mean and confidence limit (P=0.01) of the maximum, our definition of optimum, are underlined.

Desert Bitterbrush

No temperature regime was always optimum for the germination of desert bitterbrush seeds (table 31). The control optima were at colder, constant temperature regimes that only overlapped with optima for stratification. Optimum regimes for thiourea and H_2O_2 treatments were at higher warm period temperatures. The greatest overlap occurred at 10°/20° and 10°/15°C.

Cliff Rose

There were four temperature regimes, 10°/20°, 10°/25°, 10°/30°, and 15°/25°C, that always supported optimum germination of cliff rose seeds (table 31). Optima with the relatively ineffective H_2O_2 treatment tended to occur at cooler constant temperatures.

Overall Optima

If seed technologists wanted one temperature regime to use for a standard for testing all three species, 10°/20°C is the only regime with at least a 75-percent frequency for all treatments and all species.

Comparison of Germination-Temperature Profiles to Seedbed Temperatures

We have divided the temperature regimes used in the 55-temperature profile into four categories: moderate, widely fluctuating, colder, and warmer than moderate (fig. 6). These divisions of seedbed temperatures do not refer to the requirements of any one species but are based on the results of intensive studies of environmental parameters controlling germination and establishment in field seedbeds. These studies used micro-environmental monitoring techniques to determine parameters that generally allowed germination and growth of herbaceous species (Evans et al. *1970*, Evans and Young *1970* and *1972*). Essentially, if a species does not have the inherent potential to germinate well at moderate seedbed temperatures, it will be overwhelmed by competition from herbaceous weed species. An alternative strategy would be exceptional germination at colder-than-moderate temperatures to get a headstart on competing species. Germination at widely fluctuating temperatures has an important bearing on seed placement in the

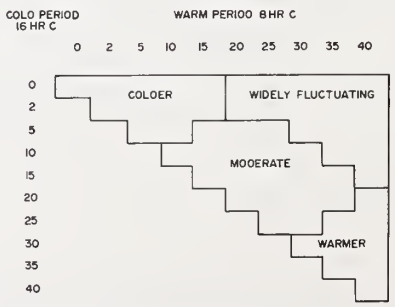

Figure 6.--Categories of seedbed temperatures used for comparison with germination profiles.

Table 31.--*Frequency of optimum temperature regimes for germination of antelope bitterbrush, desert bitterbrush, and cliff rose seeds incubated at 55 constant and alternating temperature regimes with treatments of control, stratification, thiourea, or hydrogen peroxide*

Antelope bitterbrush-Frequency of optimum

Cold period temperature (°C) 16 hours	Warm temperature (°C) 8 hours									
	0	2	5	10	15	20	25	30	35	40
0					50	25	25	25		
2				25	75	75	25	25		
5				25	75	100	25	25		
10				25	75	75	75			
15					25	25				
20										
25										
30										
35										
40										

Desert bitterbrush-Frequency of optimum

	0	2	5	10	15	20	25	30	35	40
0										
2										
5			25				25			
10				50	50	75	50	50		
15					50	75	50	50		
20						50	25	25		
25										
30										
35										
40										

Cliff rose-Frequency of optimum

	0	2	5	10	15	20	25	30	35	40
0							25			
2						25	75	25		
5						75	75	25		
10				25	25	100	100	100		
15					25	75	100	50		
20						25	50	25	25	
25										
30										
35										
40										

seedbed because the greatest diurnal fluctuations occur on the soil surface. Germination in this category also can lead to early establishment and escape from competition. Germination at warmer-than-moderate temperatures is of little value unless a weed control treatment is used to reduce competition from previously established herbaceous species.

All three of these valuable browse species are relatively poor germinators in all categories of seedbed temperatures (table 32). The best germination obtained is under 60 percent. Seeds of these species are moderately to very expensive, and these low germination percentages make it vital that land managers use optimum revegetation techniques to obtain adequate seedling establishment.

Antelope Bitterbrush

Antelope bitterbrush seeds have nearly equal germination with all types of germination enhancement at colder-than-moderate and moderate seedbed temperatures (table 32). This is a very unusual germination pattern compared with other species we have subjected to similar analysis. The frequency of temperature regimes with some germination drops slightly, but stays above 90 percent. A similar response is carried over to the widely fluctuating regimes where some germination occurs at all temperature regimes with all forms of enhancement. Only at warmer-than-optimum temperatures is germination greatly reduced. Thiourea consistently gave the highest average germination in each category, followed closely by stratification.

Desert Bitterbrush

Germination responses of desert bitterbrush were different from those noted for antelope bitterbrush. Germination at colder-than-moderate or widely fluctuating seedbed temperatures was roughly one-half of the mean for moderate temperatures. Again, warmer-than-moderate seedbed temperatures greatly depressed germination. Except at warmer-than-moderate temperatures, stratification led to the greatest average enhancement of germination, followed by roughly equal effectiveness of thiourea and H_2O_2 treatments. It is important to note the relative enhancement of germination over control treatments for antelope and desert bitterbrush. For antelope bitterbrush seeds, thiourea treatment resulted in an average of 64 percent greater germination than the untreated seeds. For desert bitterbrush, stratification resulted in a 95-percent average enhancement in germination results unless natural stratification occurs.

Cliff Rose

Cliff rose seeds follow a pattern of germination in relation to seebed temperatures that is similar to desert bitterbrush. Stratification and thiourea similarly enhanced germination in all categories. Pretreatment with H_2O_2 increased the frequency of colder-than-moderate regimes that had some germina-

Table 32.--*Comparison of the mean germination and regimes with some germination at four seedbed temperature regimes: moderate, colder, warmer, and widely fluctuating temperatures for antelope bitterbrush, desert bitterbrush, and cliff rose seeds. Four treatments are compared: control, stratified, thiourea, and hydrogen peroxide*

Species and treatment	Moderate		Colder		Warmer		Widely fluctuates	
	Mean	Some germination	Mean	Some germination	Mean	Some germination	Mean	Some germination
	Percent							
Antelope bitterbrush								
Control	16	95	17	91	3	44	25	100
Stratified	39	100	42	91	4	56	33	100
Thiourea	54	100	58	91	12	78	42	100
Hydrogen peroxide	32	100	25	91	1	11	19	100
Mean	35		36		5		30	
Desert bitterbrush								
Control	4	79	2	36	(1)	11	1	44
Stratified	58	100	43	91	6	35	25	75
Thiourea	38	100	11	91	8	33	20	88
Hydrogen peroxide	32	100	11	91	5	44	20	94
Mean	33		17		5		17	
Cliff rose								
Control	11	100	0	0	2	44	5	69
Stratified	49	100	22	82	18	100	39	100
Thiourea	49	100	26	82	10	78	40	100
Hydrogen peroxide	21	100	2	27	2	22	5	62
Mean	30		13		8		22	

[1]Less than 1 percent.

tion, but hardly raised the average germination. Again, the relative enhancement of stratified over control germination was large, averaging an increase of 87 percent.

DISCUSSION

There is no question that antelope bitterbrush, desert bitterbrush, and cliff rose are very valuable browse species, and that the successful revegetating of depleted ranges with these species would be of great value to land managers. Large scale seeding of these species has seldom resulted in successful seedling establishment. Where should research dollars be invested to solve this problem? Among the alternatives are: (1) substitute other native or exotic species that are easier to culture, (2) develop effective rodent repellents so the seeds could be fall seeded for natural stratification, (3) breed plants that modify the germination requirements, (4) develop practical method of seeding stratified seeds, (5) perfect the H_2O_2 technique, or (6) develop procedures for the use of thiourea to break dormancy as a "restricted" pesticide. The concept of restricted pesticide classification and use is that even when used as directed, the pesticide can be dangerous to the user or cause damage to the environment. To counteract the inherent dangers in the use of these pesticides, users are required to complete special training sessions before being certified to use the material.

All of these alternatives exist in different time frames from immediate application to distant possibilities. Because of these differences, they probably all should receive some research priority. Unfortunately, most native browse species that could be suggested as possible partial alternatives to antelope bitterbrush are also members of the Rosaceae family and have just as complicated germination strategies. Curlleaf mountain mahogany (*Cerocarpus ledifolius* Nutt.) is a good example (Young et al. *1978*). A source of browse species outside the Rose family may be found in the genus *Eriogonum*. There is considerable resistance to the introduction of exotic species on public rangelands and few candidates exist for evaluation, but the possibility should be explored.

Enough antelope bitterbrush seeds germinate without germination enhancement to suggest that through hybridization and selection, plant breeders might be able to greatly increase germination and reduce the strict stratification requirements. This is a long term project, but certainly should be included in programs to shift seed collection of these species from native stands to seed orchards.

There are many constraints on the seeding of moist, stratified seeds, both from a mechanical handling standpoint and from the biological requirements. Essentially, you can only seed prestratified seeds in a seedbed that is conducive to continued germination. This means that drilling would be limited to short periods of time when temperature and moisture conditions permit and are satisfactory in seedbeds. These seedbed conditions would have to be predicted because of the time required for stratification and the loss of viability with prolonged stratification. Despite all these drawbacks, stratification is the

only germination enhancement technique available for many species. Development of drills to handle moist seeds should continue.

If workable rodent repellents could be developed, fall seeding of bitterbrush and cliff rose seeds probably is the most desirable alternative. Pesticide restrictions have greatly limited the potential materials for use as repellents, and one should remember that any time a chemical is placed in close proximity to a seed, there is a distinct possibility of influencing germination. Equally important with the development of repellent is the continued study of rodent-seed ecology. The complex interaction of rodents and antelope bitterbrush seeds is well known. We assume that a similar relation exists for desert bitterbrush and cliff rose seeds under natural conditions. An unexplored possibility for enhancing regeneration of these species is to manipulate rodent populations or artificially feeding seeds into the rodent caching cycle with or without subsequent control of rodents.

Hydrogen peroxide offers an alternative method of enhancing germination of the bitterbrush species. Stratification gives a better enhancement of germination than hydrogen peroxide, especially for cliff rose seeds. The advantages for hydrogen peroxide are a shorter treatment time is required and the seeds can be dried. If we understood the nature of germination enhancement from hydrogen peroxide treatments, it might be possible to perfect the methodology to increase the germination enhancement.

Practically, thiourea, the ideal germination enhancer for bitterbrush seeds, is a dead issue. The only reason the treatment has survived pesticide regulations this long is that germination enhancement exists as an obscure use of chemicals. Virtually all State and Federal land management agencies have outlawed the use of this material as a dormancy breaker and, unless valid experimental evidence is produced refuting the production of cancer in laboratory animals, these restrictions are necessary and reasonable.

In the final analysis, we know a great deal about the germination of bitterbrush and cliff rose seeds. We also know that a great deal of work is required to develop this knowledge into a form that adequately answers the problems land managers face in trying to revegetate rangelands with these species.

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